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DEVELOPMENT OF THE HELVELLINEAE

I. HELVELLA ELASTICA

W. A. McCubbin

(WITH PLATES XIV–XVI AND ONE FIGURE)

Our knowledge of the developmental stages of the Helvellineae has been restricted to the Geoglossaceae, and is mainly due to the researches of DITTRICH (**9**) on *Leotia gelatinosa* and *Mitrula phalloides*. Practically nothing is known of the ontogeny of the Helvellaceae and Rhizinaceae. DITTRICH'S investigations on the Geoglossaceae showed, contrary to the opinion formerly held, that these forms, in their young stages at least, were unmistakably angiocarpous. He discovered that the young fruiting body of Leotia was surrounded by an envelope of hyphal filaments, which later gelatinized, and was then disrupted by the expanding ascoma beneath. In *Mitrula phalloides* the phenomena were quite similar, but among the Helvellaceae which he examined there were no stages young enough to enable him to decide as to the presence or absence of an envelope. In Mitrula the ascogenous hyphae were found to originate from hyphae which were differentiated in the central part of the fruiting body. These hyphae are long, stain readily, and are closely massed, while their nuclei are large, with a prominent nucleolus and a thin chromatin thread. From these filaments the ascogenous hyphae grow toward the hymenial layer, where a rapid branching takes place, succeeded by the formation of asci.

DURAND (**10**), in his admirable monograph on the Geoglossaceae, makes reference to DITTRICH'S investigations on the envelope in Leotia and Mitrula, and remarks, "observations of my own on several different species, before I learned of DITTRICH'S work, point unmistakably to the same conclusion." DURAND states that he found a veil in *Mitrula phalloides*, *Microglossum viride*, *Cudonia lutea*, and *Spathularia velutipes*, but "sections of quite young ascomata of *Geoglossum glabrum*, *Gleoglossum difforme*, and *Trichoglossum velutipes* have shown no traces of such a membrane." Finally he affirms the belief that "when the development of the Discomycetes shall be better understood, it will be found that in none of them, not even in the Helvellineae, is the hymenium exposed from the first."

An obstacle to the ready solution of this and other details of ontogeny is, as DITTRICH has already pointed out, the difficulty of obtaining young stages either by collection or culture. BREFELD (**3**) made attempts to cultivate the spores of several Helvellineae, but though a mycelium was produced in some cases, no fruiting bodies could be obtained, and often germination did not take place at all. MOLLIARD (**16**) had better success with spores of *Morchella esculenta*, from which he was able to procure a vigorous mycelial growth. This mycelium produced conidia identical with those of Costantinella, and when planted in a compost of apples gave rise to a couple of small fruiting bodies of the morel.

In regard to the taxonomy of the Helvellineae various criteria have been adopted. SCHROETER'S (**17**) classification bases the distinction between this group and the Pezizineae on the supposed gymnocarpous origin of the fruiting body in the former and the angiocarpous in the latter. BOUDIER (**2**), in endeavoring to construct a natural classification of the Discomycetes, adopts a feature other than angiocarpy or gymnocarpy as a basis. He looks upon the Helvellineae as a polyphyletic group: one part, comprising the Helvellaceae and the Rhizinaceae, being placed in that division of the Discomycetes (Operculés) whose asci open by an apical cap; and the other, consisting of the Geoglossaceae, being relegated to a second division (Inoperculés) whose asci open merely by a pore. BREFELD found on examination of several Discomycetes that when an ascogonium is present the ascogenous hyphae appear quite early, but when the fertile filaments spring from ordinary hyphae, as he stated to be the case in several of the Helvellineae and some Pezizas, the ascogenous hyphae are differentiated at a much later stage. He thought that as the ascogonium occurs in simple forms but not in the more specialized, and that as the specialized forms themselves differed, according to the species, in the time at which the ascogenous hyphae appeared, the gradually later and later differentiation of the fertile filaments would form a very good basis for the arrangement of the Discomycetes in a natural series, at the end of which the Helvellineae would probably stand.

The following investigations have been undertaken for the purpose of enlarging our knowledge of the ontogeny of the Helvellineae, and in the hope that fuller information will be of assistance in dealing with the phylogeny of the group. The complex fructifications of the Helvellineae could scarcely be expected to furnish promising material for working out some of the cytological problems that have been attracting attention in certain other divisions of the Ascomycetes, involving the sexuality of the Ascomycetes and their affinities with other Thallophyta, yet certain phenomena have come to light that prove interesting and suggestive.

Rather complete series of several genera of the Helvellineae have been accumulated and are being studied. Any theoretical considerations will be deferred to a later paper.

Helvella elastica

MATERIAL AND METHODS.—The young stages of the material examined were taken from a bank of loose damp sand in High Park, Toronto, and were collected in July 1908. They were fixed in several ways and cut in series in paraffin. Staining was tried with Erlich's hematoxylin, iron hematoxylin, safranin, eosin, rubin S, Flemming's triple stain, methylene blue, and several others. Iron hematoxylin and Flemming's triple stain gave the best results, the former making the nuclei prominent and the latter bringing out the general features. Macerations were also found to be valuable, the crushed material being stained on the slide with safranin or methylene blue.

Some tentative attempts were made to produce the mycelium of several Helvellineae from spores, with the hope of arriving at the young stages of the fruiting bodies by laboratory cultures. The results, however, are as yet insufficient to justify any statement.

I would here acknowledge my indebtedness to Professor J. H. FAULL for material and advice throughout this investigation, and to Mr. R. B. THOMSON for many courtesies.

MYCELIUM.—The mycelium of *Helvella elastica* is easily obtained by washing the earth surrounding young fruiting bodies. It consists of long, sparsely branched, interwoven filaments about 0.03–0.04^{mm} in diameter. These filaments are often connected by anastomoses (*figs. 3–5*). The cells are multinucleate, containing 2–16 or more small densely staining nuclei. These are frequently arranged in pairs (*figs. 3, 4*). Often one finds a pair separated by a septum, a condition of affairs similar to this being described by STOPPEL (**21**) for *Eremascus fertilis*. Metachromosomes such as CLAUSSEN (**7**) describes for Boudiera are also found here. Two or more are visible lying parallel to the cross walls of the thread, and appear to be more conspicuous near the end of a filament than in its older parts.

THE ASCOMA.—Here and there a specially vigorous growth of the mycelium produces knots or clumps (the fruiting bodies), the cells of which are shorter, thicker, and more branched than those of the surrounding filaments. The earliest stages of the fruiting bodies procured were about 0.5^{mm} in diameter. At this stage the young Helvella consists of a short thick stem spreading out insensibly into the mycelial growth of the substratum, and surmounted by a round bulbous cap of slightly larger diameter than the stem (*fig. 6*). There is at this period no indication of fertile filaments. A membrane and a palisade layer inclose the whole fruiting body, but the palisade hyphae are not yet well differentiated. In stage 2 (diam. 1^{mm}, *fig. 7*) storage cells appear, the palisade layer shows more regularity, while the membrane has been much broken by the rapid growth. Stage 3 (diam. 1.25^{mm}, *fig. 8*) shows the beginning of paraphyses on the site of the hymenium, an increased number of the storage organs, and the presence of a few ascogenous hyphae. The membrane is now represented merely by a few flakes. The hymenium does not grow rapidly at first, however, being outstripped in this respect by the stem and sterile part of the cap. As a result the hymenial surface may assume a flat or even concave shape, as shown in stage 4 (*figs. 9, 66*). Here the membrane has almost disappeared, only a few degenerate threads or masses of cells being distinguishable. The paraphyses are now numerous and the ascogenous hyphae are beginning to branch or even to form hooks. In *fig. 10* the fruiting body has assumed the characteristic saddle shape of the Helvellas. There has been from stage 4 a rapid enlargement of the hymenial surface, which takes place, however, as DITTRICH has pointed out, with considerable irregularity, thus accounting for the peculiar shape of the adult ascoma.

THE PALISADE LAYER.—Surrounding the entire fructification in early stages, and persisting throughout life on all but the hymenial surface, is a "palisade layer." This layer is formed from club-shaped ends of the hyphae, which arrange themselves closely and evenly at right angles to the surface. In early stages this layer is not well differentiated. Later on it becomes more regular, its threads take on a more pronounced club shape, and the cells become filled with deeply staining contents.

THE MEMBRANE.—The envelope which covers the fruiting body in its early stages arises from the palisade layer. Many of the club-shaped hyphae of the latter continue to grow out beyond the general surface, then turn at right angles, and interlacing in every direction along the surface form a matted web 2–8 threads in thickness. This membrane is very transitory, however, and undergoes degeneration at an early period. Its protoplasm takes on a granular appearance, the cell outlines become indistinct, and finally the whole disintegrates into a deeply staining mass in which the nuclei are the most prominent feature. Long before this process is complete, however, the rapid growth of the underlying tissue bursts the emvelope so that it adheres in flakes (*figs. 57, 58*). Then the paraphyses and intercalary palisade hyphae pushing out to the surface complete the separation and all traces of it are cast off.

DURAND, in speaking of this veil in *Microglossum viride*, states that "when the veil seems to break up into fragments, there are indications that the hymenium first appears through *a pore at the apex*." This phenomenon has been homologized with the opening of the apothecium in Ascobolus. But the coverings of Spathularia, Leotia, and Mitrula break up irregularly without any indication of an apical pore, and in *Helvella elastica* also it breaks irregularly. Moreover, in some forms a veil may be altogether lacking. Indeed I am able to state definitely, from observations on a very complete series of stages, that *Geoglossum hirsutum* shows no trace whatever of such a structure.

THE PARAPHYSES.—In sections of young ascomata of *Helvella elastica* the hymenial surface is not yet differentiated, being quite similar to that in other parts of the fruiting body, and covered by the common palisade layer and external veil. Very early, however, the paraphyses begin to appear, and as these force their way upward through the palisade filaments the veil is broken and thrown off. The paraphyses arise from ordinary hyphae in the interior of the fruiting body, and are in the early stages quite similar to the filaments of the palisade layer, so that the hymenium can only be distinguished at this period by the greater number and the closer and more regular arrangement of its units. Later on, however, the paraphyses elongate and become thinner, less bulbous, and more closely packed. In this older condition they are filled, especially near their ends, with dense deeply staining contents in which the nuclei seem to have degenerated. They are also septate and their more basal cells show two or more small dense nuclei. The hyphae which give rise to paraphyses may be traced for some distance into the hyphal mass of the cap, and indeed in many cases nearly to its lower surface.

STORAGE BODIES.—A conspicuous feature in sections of *Helvella elastica* is the presence of large cellular bodies filled with contents, and distributed irregularly throughout the whole of the fruiting body except the stem. These bodies are quite large, attaining sometimes 20–30 times the diameter of the surrounding hyphae, but they vary exceedingly in size and shape. Sometimes they form a chain of three or four connected cells, or they may consist of a single mass with irregular protuberances, or they may be merely filaments enlarged for a considerable portion of their length. They often occur in groups, the individuals of which are unconnected.

In most of the ascomata sectioned the protoplasm of these bodies had shrunken somewhat from the cell wall. It is coarsely granular and stains deeply. Nuclei are present in numbers varying from 1 to 20 or more. There are usually present either one or two large nuclei (*figs. 46, 48, 50, 63*), or a number of smaller ones, though both sizes may occur in the same cell (*fig. 46*). Moreover, as shown in *figs. 46–56*, which are taken from a single representative ascoma, all stages intermediate between these extremes may exist. The large nuclei are loosely reticulate in structure, while the smaller are dense and stain deeply. The latter show in many cases a tendency to occur in masses (*figs. 49, 52, 54, 56*). Another conspicuous feature among the nuclei of these large bodies is their frequent arrangement in pairs (*figs. 47, 53, 55, 61*).

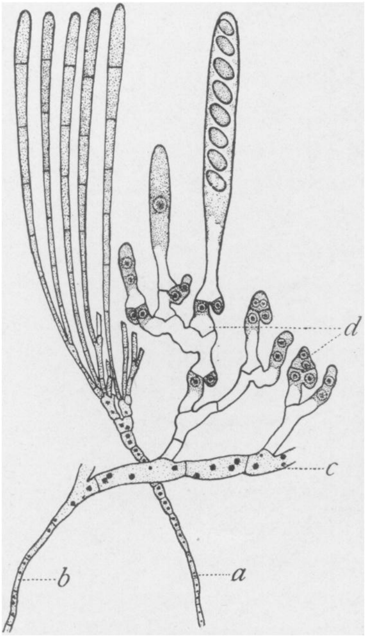
The general occurrence of these bodies throughout the cap would seem to indicate a vegetative function. They are to be found at the base of the hymenium giving off paraphyses, or within the hymenial layer, in which case they are surmounted by one or more paraphyses (*figs. 43, 64*); or they may force their way to the surface, appearing there as enlarged clublike processes plainly having the jointed structure of the paraphyses. The ends of these processes are often found ruptured and the contents, like lava from a crater, overflowing the neighboring surface. These enlargements are further found all through the subhymenial hyphal mass, and many of the palisade hyphae originate from those near the lower surface (*fig. 60*). In addition to that, these bodies are found connected with the fertile filaments either remotely in the subhymenial layer or else having the ascogenous hyphae proceeding directly from them. Often part of an ascogenous hypha, at quite as late a stage as the formation of the hooks, is greatly enlarged, the similarity of stain and nuclear structure leaving no doubt as to the close resemblance of these swellings to the bodies in other parts of the ascoma (*figs. 36, 62*). In very young stages of development these bodies are not present, but they appear quite early in the history of the ascoma, as previously mentioned. At the time when the asci are fully formed, they are usually empty, their connections have vanished, and their walls are shrunken and degenerate. Observations on a considerable number of specimens indicate that these bodies vary with the individual, being largest and most abundant in vigorous plants. They vary also in the individual, serial sections showing one-half of the fruiting body well supplied with them and the other containing scarcely one.

With the foregoing data in hand, it seems most reasonable to regard these peculiar structures as organs for the storage of food material.

ASCOGENOUS HYPHAE.—When the fruiting body is about 1.25^{mm} in diameter, the first hyphae which are undoubtedly ascogenous make their appearance. Some of the hyphal threads form a matted web a short distance below the layer of paraphyses (*fig. 59*). The threads of this web are long, straight, multinucleate, sparsely branched, and twice or thrice the thickness of the ordinary filaments. It is from these that the vertical ascus-bearing threads arise.

A comparison with what DITTRICH records for Mitrula shows that in Helvella there is a much later differentiation of the fertile filaments.

Moreover, they are not traceable to any distinct source, as were those in Mitrula, but arise merely from the ordinary hyphal threads of the fruiting body. This is an agreement with BREFELD'S observations on several species of Morchella, Helvella, and Geoglossum, as well as *Leotia lubrica* and *Peziza Sclerotiorum* (Heft IV, 130). According to him the ascogenous hyphae may arise from the common filaments of the fruiting body and even from those which had formerly produced paraphyses.



Hymenium of *Helvella elastica* (semi-diagrammatic): *a*, sterile hypha producing paraphyses; *b*, undifferentiated fertile filament; *c*, enlarged fertile filament in the sub-hymenial layer; *d*, ascogenous hyphae showing the succession of hooks, the fusion of terminal and antepenultimate cells, and the formation of the ascus (the unshaded parts are empty).

In *Helvella elastica* there is frequently a thickening of the sterile filaments before they form the profusely branched mass of paraphyses, but such enlargements have no connection with those occurring in the ascogenous hyphae. The cells of the former are short, bulbous, and usually binucleate, while in the fertile threads they are long, uniform, and multinucleate (see *text fig.*). Moreover, no connection can be traced between the two, nor can any paraphyses be seen coming from the ascogenous filaments.

From the fertile subhymenial layer lateral branches are given off in rather scanty numbers, and these grow toward the layer of paraphyses, where they branch repeatedly. The end cells of these lateral branches contain an abundance of deeply staining protoplasm and 2–5 nuclei, the usual number, however, being 2 (*figs. 11–19*). The whole energy of growth seems to be concentrated in this end cell, for usually those behind it are completely empty, and long before branching has been completed even the walls disappear. DITTRICH notes the same phenomenon in *Mitrula phalloides.* It is evident that in these cases the developing ascus must be nourished by diffusion from the surrounding cells. As growth proceeds in the vertical branch, transverse walls are formed at intervals along its course (*figs. 11–18*). When nuclei and protoplasm happen to be cut off by these walls, a lateral branch may be produced from the cells thus left behind (*figs. 12, 16*). Finally the end cell forms a hook and its two nuclei divide to form four. Then follows a septation of the hook into three cells, a daughter of each of the mother nuclei remaining in the penultimate cell and the other two being distributed to the terminal and antepenultimate respectively. From the penultimate cell a process now arises into which its two nuclei wander (*figs. 20, 27.*)

Heretofore in the Ascomycetes which have been investigated there has come into consideration only one hook (where hooks exist), the process from which becomes the ascus. Here, however, it is curious to note that the process from the first hook may proceed to form a second. Its two nuclei, instead of fusing, divide again, the resulting four being distributed in the second hook as in the first. Indeed this formation of successive hooks may go on for some time, as many as six having been observed on one ascogenous hypha. The last-formed process then becomes the ascus, its nuclei fusing to form the primary ascus nucleus, and from this spore nuclei are produced by the usual three successive divisions. One important feature is made strikingly evident by these hooks, namely the conjugate division of the nuclei in the ascogenous hyphae. It has been quite evident from my observations that the two nuclei which fuse in the young ascus are directly descended by conjugate division from the two which normally occupy the end cell of the ascogenous hypha as it first arises from the subhymenial layer.

Another phenomenon of interest is the "fusion" or "anastomosis" that quite frequently takes place between the terminal and antepenultimate cells. The nucleus of the antepenultimate cell passes into the former, and from thence the two nuclei wander into a process which invariably arises from the terminal cell (*figs. 33, 34, 36–38, 40*). It will be readily seen that this process with its two nuclei is the direct equivalent of that which originates from the penultimate cell, and indeed it conducts itself in exactly the same way, forming further series of hooks in which anastomoses may likewise take place, all the resulting processes finally ending in asci (*text fig.* and *figs. 32, 38, 40–42*).

Occasionally there has been obviously no fusion of the terminal and antepenultimate cells, yet a branch has arisen from the former. As in such cases the antepenultimate cell retains no nucleus, it is probable that pairing of the daughter nuclei has taken place before the cutting off of a binucleate penultimate cell, a case quite comparable to that observed by MAIRE (**15**) in *Galactinia succosa*.

Summary

The mycelium of *Helvella elastica* is subterranean. Its cells are multinucleate.

The fruiting body arises from clumps of thick short-celled filaments.

This fruiting body is quite early surrounded by an envelope which is transitory and breaks up irregularly. Closely associated with the veil in early stages, but persisting throughout the life of the fruiting body, is an external layer of club-shaped palisade hyphae.

Certain large irregular cells occurring in all parts of the fruiting body (except the stem) apparently have the function of storage organs.

The "ascogenous hyphae" arise as a clearly differentiated subhymenial complex of filaments. From this layer grow out vertical branches whose end cells contain usually two nuclei. Hooks are formed by these end cells, while the proximal part of the branch degenerates.

The process from the first hook, without fusion of its two nuclei, may proceed to form a second and similar hook. From this second a third may arise, and so on, up to the number of at least six, the process from the last becoming the ascus after nuclear fusion.

In any hook of such a series a "fusion" or "anastomosis" of the terminal and antepenultimate cells may take place, the nuclei of both passing into a process arising from the former. This process is equivalent to that springing from the penultimate cell, and conducts itself in the same way.

The two nuclei which fuse to form the primary ascus nucleus are directly descended by conjugate division from the two which occupied the end cell of the young ascogenous hypha.

No structure having the conventional form of an ascogonium was found.

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EXPLANATION OF PLATES XIV–XVI

FIGS. 1–5.—Parts of mycelium. ×300.

FIGS. 6–10.—Stages showing development; actual length indicated.

FIGS. 11–19.—Young ascogenous hyphae before formation of hooks. ×360.

FIGS. 20–27.—Formation of first hooks. ×360.

FIG. 28.—Young ascogenous hyphae arising from enlarged filament in the subhymenial layer. ×360.

FIGS. 29–31.—Formation of successive hooks. ×360.

FIGS. 32–34.—Fusion of antepenultimate and terminal cells. ×360.

FIG. 35.—Drawing from maceration showing three successive hooks ending in young ascus.

FIG. 36.—Enlarged ascogenous hypha, the enlargement involving four successive hooks. ×360.

FIG. 37.—Swollen hook from same group as *fig. 36*, showing fusion of terminal and antepenultimate cells.

FIGS. 38, 40–42.—Fusion of terminal and antepenultimate cells.

FIG. 43.—Storage body in paraphyses layer.

FIGS. 44, 45.—Storage bodies from palisade layer on under surface of cap. ×360.

FIGS. 46–56.—Storage bodies in interior of the ascoma showing size and arrangement of the nuclei. ×360.

FIG. 57.—Young fruiting body with remnants of the envelope adhering. ×60.

FIG. 78.—Part of surface of *fig. 57*, showing palisade layer and fragments of the membrane. ×300.

FIG. 59.—Section through the cap. ×100.

FIG. 60.—Filaments of the palisade layer arising from storage bodies. ×300.

FIG. 61.—Storage bodies (outlined in ink) showing paired nuclei. ×300.

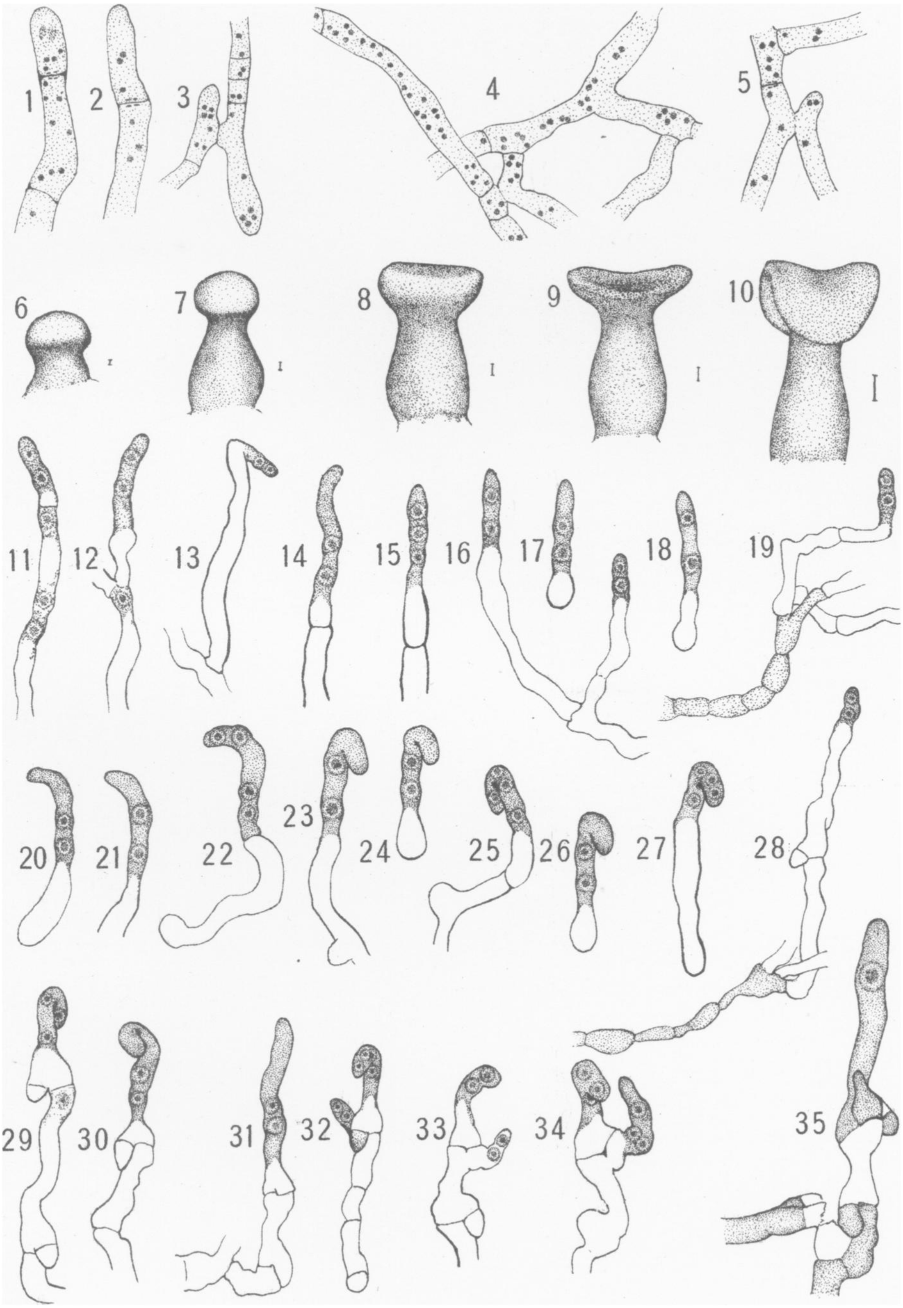
FIG. 62.—Enlargement of ascogenous hypha involving several hooks (see *fig. 36*).

FIG. 63.—Storage cell with two large and several small nuclei (*fig. 46*).

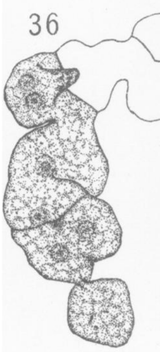
FIG. 64.—Storage bodies in the hymenial layer ending in paraphyses.

FIG. 65.—Young ascogenous hypha with two successive hooks.

FIG. 66.—Section of young fruiting body with concave hymenial surface.



McCUBBIN on HELVELLINEAE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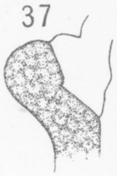
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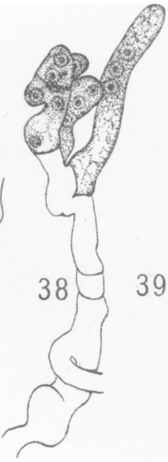
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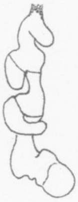
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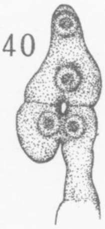
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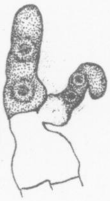
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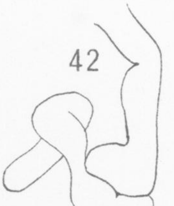
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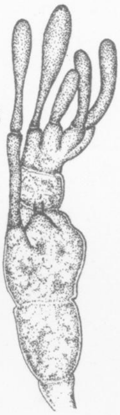
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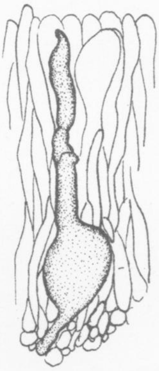
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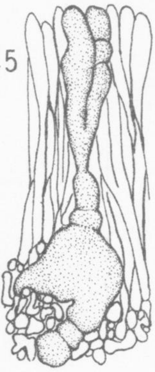
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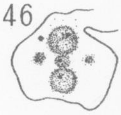
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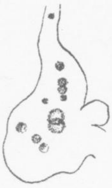
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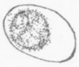
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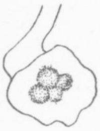
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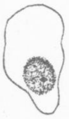
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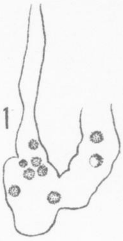
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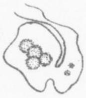
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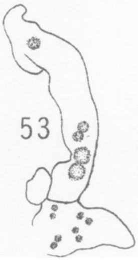
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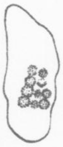
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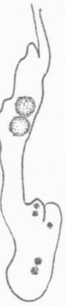
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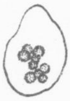
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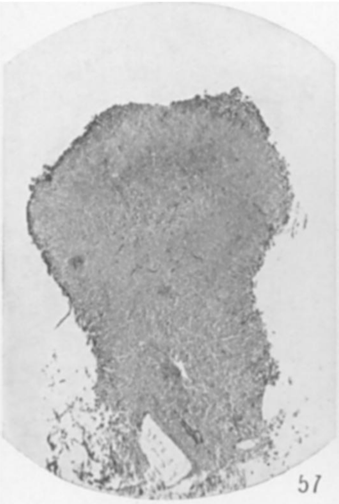
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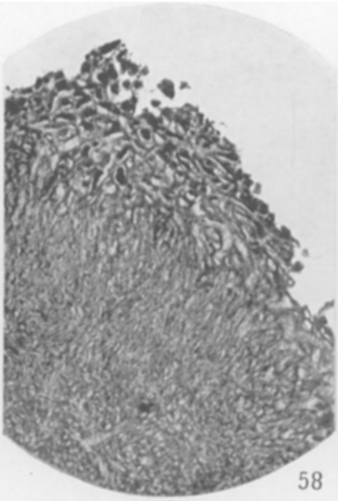
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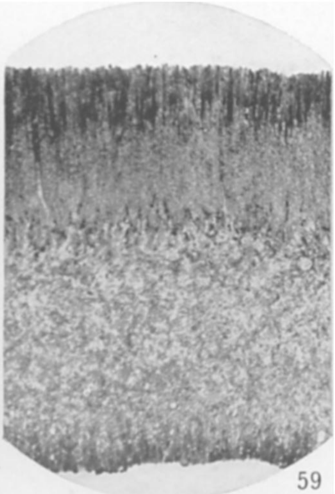
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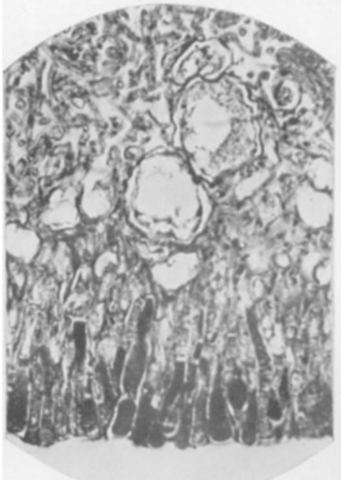
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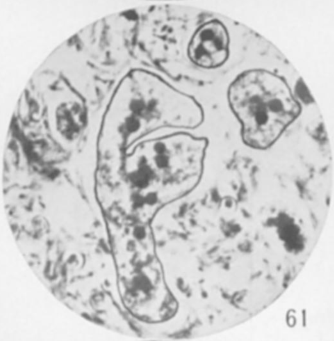
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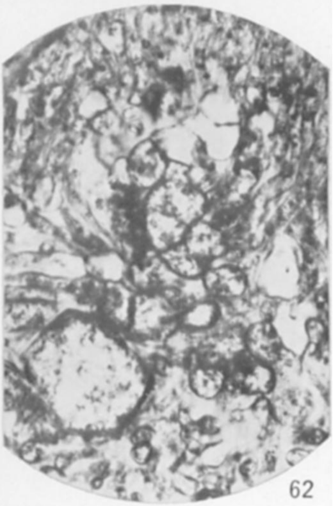
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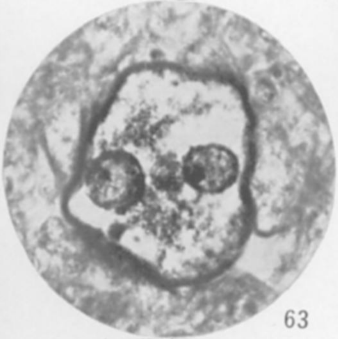
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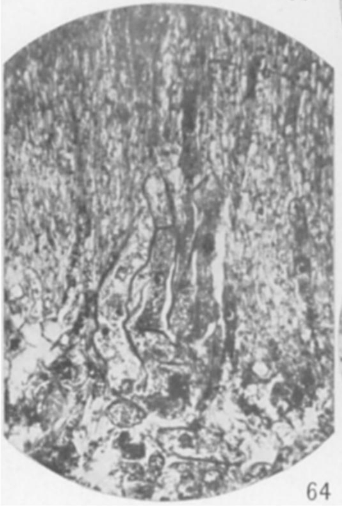
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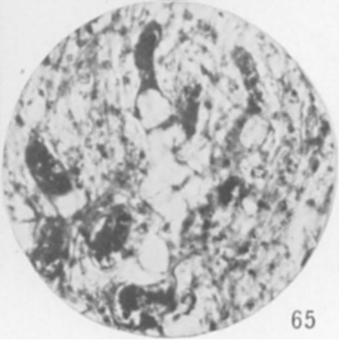
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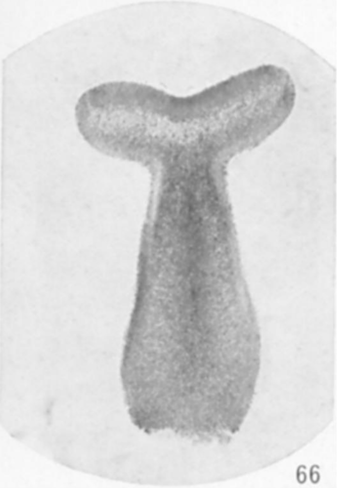
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